THE STRUCTURE AND METAMORPHOSIS OF THE ALIMENTARY CANAL OF THE LARVA OF PSYCHODA ALTERNATA SAY.*

By LEONARD HASEMAN.

The changes which take place in the digestive epithelium of insects after feeding, and in connection with the molting periods, have been but little studied, though in the cases known the phenomena are of great interest. In some insects partial, in others, total regeneration of the mid-intestinal epithelium has been found to occur after each taking of food. In other instances it is the changes associated with molting which have attracted attention. It was with a view of studying the morphological changes in the epithelium at the two periods and of correlating the results with those of previous workers that this study of the larva of Psychoda alternata was undertaken.

A review of the literature shows that but little has been done along these lines with larval forms. Aside from the work of Van Gehuchten ('90 and '93) on Ptychoptera contaminata, Mobüsz ('97) on Anthrenus and Folsom and Wells ('06) on Collembola, we find only scattered references here and there in more general papers on the digestive system. Psychoda alternata has been selected for the present work because of the ease with which it can be secured and bred throughout the year, its wide distribution, its convenient size for work and the fact that it is one of the most generalized Diptera.

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THE STRUCTURE OF THE ALIMENTARY CANAL.

The alimentary canal of the larva of Psychoda alternata is a straight tube extending from the mouth to the anus, without folds, except during bodily contraction when a slight one is formed in the region of the small intestine. Aside from the attachment of strong pharyngeal muscles and the Malpighian

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*Contribution from the Entomological Laboratories of Cornell University.

vessels, the surface of the canal for its whole length is unbroken (Fig. 1). From the exterior the division into fore-, mid- and hind-intestine is distinctly marked. The short, much constricted fore-intestine extends back to the third thoracic ganglion. Here, by means of a strong esophageal valve, it connects with the very large mid-intestine, which in turn extends back to the sixth abdominal segment, where the somewhat constricted hind-intestine begins.

The opening of the mouth is on the ventral surface of the anterior part of the head. The clypeus and recurved labrum form a rostrum over and in front of it. The labrum bears, on either side of its anterior recurved margin, a fan of bristling hairs (Fig.3 lr.) The area between these fans is armed with numerous posteriorly directed, strong setae and minute serrate chitinous plates. Posterior to this area is a strong V-shaped plate and laterad of it, along the margin, a pair of mesally directed triangular plates. Behind the V-shaped plate comes a group of small chitinous plates, arranged in a circle, and a series of minute setae. A pair of small plates, bearing numerous minute teeth on their mesal margins, lies laterad of this chitinous ring. Farther back is a pair of lateral tufts of setae and a second pair of oval plates.

The mandibles are strongly chitinized with numerous lateral setae, a single strong spine, with numerous minute teeth on its inner margin, and two long plumes (Fig. 3, md.) On the inner margin are two series of strong teeth, directed at an angle to each other, and a single posterior thumb-like tooth directed cephalad. The hind margin of the mandible is deeply concave to receive the anterior part of the maxilla.

The maxillae are but slightly chitinized, with four short stout teeth on their inner margin, a small median plume and a fan of long setae extending the full length of the lateral margin. The palpi are short and thick with six small papillae and numerous short setae. They are circular in outline and fit into the depressions in the hind margins of the mandibles (Fig. 3, mx.)

The labium is a fleshy lobe bearing numerous fine setae and papillae. On the anterior margin are two small tufts of short setae and behind these a crescent-shaped chitinous plate (Fig. 3, la). The sense papillae found upon the labrum, maxillae, palpi and labium are so placed as to come in contact with the food as it enters the mouth and therefore are very probably organs of taste. The setae and plumes surrounding the mouth are curved, near their tips, and so arranged as to sweep food into it when the mouth parts are in motion.

The mouth opens almost immediately into the pharynx, which is somewhat expanded dorsally and supported on its cephalo-lateral margins by curving chitinous bars (Fig. 4, ph.) Strong muscles extend from its cephalic, lateral and dorsal surfaces to their points of attachment on the chitinous surface of the head. Posteriorly the pharynx tapers rapidly into the narrow esophagus so that their point of union is hardly discernable. The esophagus is slender, uniform in diameter and extends from the subesophageal ganglion to a point opposite the third thoracic ganglion. The surface of the esophagus is free from any visible suspensory attachments and, to the unaided eye, shows rather indistinctly the arrangement of the circular muscles.

Lying alongside the esophagus, above the first thoracic ganglion, are the salivary glands. They are quite prominent, each about the size of one lobe of the brain, and strongly reniform. From the ventral end of each gland, a minute duct extends downward and forward to a point below the subesophageal ganglion, where the two from opposite sides unite to form the main salivary duct. This duct runs forward below the alimentary canal to the mouth, where, as we shall see later, it opens between the hypopharynx and labium (Fig. 4, d.)

Closely enclosing the pharynx are the commissures connecting the brain with the subesophageal ganglion (Fig. 4, com.) These commissures extend forward and slightly downward on either side until the level of the pharynx is reached when each turns rather abruptly backward and downward to the subespohageal ganglion.

Above the second and third thoracic ganglia, the narrow esophagus is telescoped into the mid-intestine forming the espohageal valve. The diameter of the tube in the region of the valve is much greater than that of the esophagus but less than that of the mid-intestine farther back (Fig. 1, es. v.) The mid-intestine normally is a smooth tube tapering slightly anteriorly from its middle and posteriorly from a point near its union with the hind-intestine. When it is gorged with food, however, its diameter may be more uniform throughout. In surface view the cellular structure of the mid-intestine stands out very distinctly even with low power magnification.

The alimentary canal and especially the mid-intestine is closely and firmly enclosed in columns of adipose tissue. Four longitudinal lateral strands extend the full length of the larva with shorter strands here and there. The adipose tissue and Malpighian vessels form a perfect cushion about the canal and in this way support it in the central part of the body cavity. When the alimentary canal is dissected out the adipose tissue adheres to it and severs its connection with the body wall, and the respiratory and nervous systems. In living larvae numerous fine tracheal branches, from the pair of dorsal longitudinal tracheae, are seen to ramify the fat bodies and send finer branches to the alimentary canal. The nervous connections with the adipose tissue and alimentary canal are much finer and more difficult to discern than are the tracheal connections. Delicate cephalad directed fibers from the large dorsal nerve, which extends caudad from the eighth abdominal ganglion, are seen to attach to the ileum just behind the Malpighian vessels corresponding to suspensory nerves described by Comstock and Kellogg, '95, for Corydalis. These fine nervous connections from below with the tracheal connections from above assist in supporting the alimentary canal.

From surface view the hind intestine is distinctly divided into ileum and colon, while the rectum is less easily made out (Fig. 1). The ileum extends from the point of attachment of the Malpighian vessels, opposite the anterior end of the sixth abdominal segment, to the middle of the seventh segment where it joins the much expanded colon. It is so much narrower than the mid-intestine on the one hand and the colon on the other that, in surface view, it stands out in sharp contrast with them. The circular muscles of the ileum are strongly developed and appear as a distinct transverse surface banding. The walls are very thin and elastic.

The diameter of the anterior end of the colon is twice that of the ileum, while posteriorly it tapers to the rectum where it is about equal that of the ileum. The walls of the colon are very thick and but slightly elastic. The circular muscles are strongly developed and are imbedded in pits in the epithelium.

The rectum is quite short, extending from a point opposite the anterior end of the eighth abdominal segment, where the canal bends ventrad, to the anus. It is narrower than the colon and the circular muscles are not imbedded in pits. Exteriorly it is developed into four distinct papillae which surround the anus (Fig. 1, a. p.)

The Malpighian vessels join the alimentary canal at the union of the mid-intestine and ileum. They are five in number, two on the latero-ventral side, two on the dorso-lateral side, and the fifth on the dorsal surface of the canal (Fig. 1, m. t.) The vessels all have an expanded reservoir-like basal portion, which in living larvae is snow-white, but in alcoholic specimens fades out (Fig. 27, c.) The two latero-ventral vessels extend far forward to a point opposite the middle of the mid-intestine where they make an abrupt turn backward for a short distance. The two dorso-lateral ones start forward but in the middle of their expanded basal reservoirs they turn abruptly upon themselves and their distal ends become closely associated with the reproductive organs opposite the middle of the colon. The dorsal tubule follows the same course, its tip lying free above the middle of the colon. Beyond the expanded basal reservoir, the vessels are much constricted and heavily charged with a reddish-brown pigment in life. The vessels are slightly motile.

Wheeler ('93) claims that the primitive number of Malpighian vessels in insects is six. Where there are less than six, he claims that the reduction is due to a loss or fusion of certain ones, while where there are more than six, he explains it as being due to a division of some of them. However this may be, it is well known that the vessels are usually paired, that is, there is an even number of them. It is rare to find an odd number of Malpighian vessels in insects. Wheeler reports seven for a Neuropterous larva, probably Chauliodes, and the same number is found in the larva of Corydalis cornuta. Five Malpighian vessels have been found in Culex and Psychoda. I find this same number in Pericoma. In Psychoda alternata there seems to be no difference in form or structure between the single dorsal vessel and the other four paired vessels. They all join the alimentary canal singly and are about equi-distant. The same number and arrangement are found in the pupal and adult stages.

Surrounding the anal opening are four prominent fleshy lobes. These are direct prolongations from the rectum and have a respiratory function. Numerous fine tracheae extend downward and forward to these, from a constriction in the large longitudinal tracheae just caudad of the vent. These lobes are slightly protractil, becoming especially prominent in larvae that have been submerged for a considerable length of time. They are homologous with the anal tracheal gills of other insects. Vaney ('02) gives a figure showing the connection of the tracheae with these lobes in a Psychoda larva where the tracheae are far more prominent than in Psychoda alternata.

The chitinous intima of the mouth cavity is quite thick and continuous with that of the mouth parts and surface chitin of the head (Fig. 5, in.) The epithelium is thin except beneath the minute serrate plates on the anterior surface of the labrum where the cells are very long and slender. In longitudinal sections the hypopharynx and epipharynx are very prominent. The epipharynx is closely associated with the back part of the labrum and bears setae and taste papillae (Fig. 5, eph.) The hypopharynx lies immediately above the labium. Its intima is very thick and dark and near its base are strong setae protruding into the mouth of the pharynx (Fig. 5, hy.)

From the back part of the mouth the food passes directly into a large chamber, the anterior part of the pharynx (Fig. 2, ph.) The dorso-cephalic wall of this chamber is very thin and flexible to accommodate varying quantities of food. On either side of this chamber near its anterior end are two strong dorsally directed curving chitinous bars. These bars from opposite sides almost meet above and below and serve as a support for the flexible walls and at the same time bear a series of long yellow ventro-mesally directed chitinous setae which give them a comb-like appearance (Fig. 6, ph. b.) These comb-like structures across the entrance to the alimentary canal function as strainers in keeping out large foreign bodies. The pharyngeal chamber is always more or less filled with food and probably functions as a crop in which the food is mixed with the salivary secretions, by the action of the circular and pharyngeal muscles and these comb-like chitinous structures. The epithelium in this part of the pharynx is quite thin, while the chitinous intima is thick. The circular muscles in this region are by no means so strongly developed as in the caudal part of the pharynx.

The posterior portion of the pharynx is constricted so that its diameter is about equal that of the esophagus. In transverse section it appears pear-shaped, the broader portion being ventrad (Fig. 9.) It is provided with very powerful circular muscles which lie so closely together as to form almost a continuous layer. The epithelium consists of very large cells, with large oval nuclei, whose nucleoli and chromatin material stain intensely with haematoxylin. The cavity of the pharynx in this region has the shape of a Roman I, a narrow dorso-ventral slit and transverse dorsal and ventral arms (Fig. 9, l.) The intima of the dorso-ventral slit is very thick and the underlying epithelial cells are very large, cubical and with distinct cell walls. The intima lining the dorsal and ventral arms of the cavity is much thinner and the underlying epithelium is equally reduced in thickness.

The powerful circular muscles serve as constrictors for closing the lumen of the pharynx, while four sets of strong pharyngeal muscles serve as relaxers. On either side of the median portion of the pharynx are two horizontal rows of strong muscles, each row consisting of four separate muscles and a single very large anterior one. These muscles extend laterad and attach at the sides of the head. Their inner ends pass between the circular muscles and are attached to the large cubical epithelial cells by means of numerous radiating, zig-zag strands (Fig. 8, ph. m.) From the dorsal surface of the pharynx at the tips of the comb-like bars is a series of four strong muscles which extend dorsad to the surface of the head, joining it at its caudal margin. Low down on the dorso-cephalic margin of the expanded pouch-like portion of the pharynx are a number of strong muscles which extend dorso-cephalad to the surface of the head. The caudal portion of the pharynx with its heavy chitinous intima and strong constrictor and retractor muscles, must serve as a mill for crushing the food as it is passed on to the esophagus.

The pharynx ends and the esophagus begins beneath the caudal end of the brain (Fig. 4, es.) The circular muscles of the anterior portion of the esophagus completely clothe it, but the individual muscles are less strongly developed than those of the pharynx or those of the posterior part of the esophagus. Longitudinal muscles have not been found in any of the preparations. The epithelium is very thin. The cells forming it are without distinct walls and their small nuclei are arranged in definite rows along the dorsal, lateral and ventral surfaces of the esophagus. The large lateral cells of the pharynx give way in the esophagus to small cells which protrude into the lumen to form a longitudinal ridge on either side (Fig. 10, ep.) The slight mid-dorsal and ventral protrusions of the epithelium in the pharynx, persist in the anterior part of the esophagus, forming a slight dorsal and a ventral longitudinal ridge. In the median portion of the esophagus these ridges almost disappear while in the caudal region there are two dorsal and two ventral ridges (Fig. 11, ep.) These dorsal and ventral ridges are simply thickenings of the cells opposite the nuclei while the lateral ones are formed by an elevation of the cells from the muscular coat and a protrusion of them half way in to the center of the lumen. The chitinous intima of the esophagus is well developed although much less strongly than in the pharynx. It becomes much folded and is usually severed from the epithelium by fixation. On the inner surface of the infolded intima of the esophageal valve, there are to be seen, with high magnification, a number of strong spine-like setae, but these are absent in the anterior portion of the esophagus (Fig. 17). They are so directed as to resist the passage of food from the mid-intestine back into the esophagus.

The salivary glands are quite prominent, each about the size of one of the lobes of the brain (Fig. 12). They are strongly reniform so that their free ends lie almost directly above their proximal ends. When the glands are not secreting their lumina may be very large, but during active secretion they are nearly obliterated. The cells are very large and protrude into the lumen so that in sections there are deep grooves between them. They have a coarse granular and vacuolate appearance, and are usually set off by distinct walls, except during active secretion when these may become obliterated. The nucleus is very large and centrally located, with deeply staining chromatin material and a very large nucleolus. The chitinous intima is quite thick but obscured by the granular nature of the underlying cells and the secretions in the lumen. The limiting basement membrane is very delicate, but stands out distinctly.

From the ventral anterior end of the glands, ducts pass forward and downward to a point beneath the sub-esophageal ganglia where the two join to form the main salivary duct. This main duct passes forward to the mouth where it opens on the surface of the labium between it and the hypopharynx. The intima of this duct is quite delicate posteriorly while the epithelium is more prominent, but near its anterior end both the intima and epithelium are prominent. Just before the duct reaches the labium it is provided with a distinct press. The lower surface of the duct is attached to a strong chitinous process from the intima of the labium while a pair of very strong muscles is attached to the dorsal surface (Fig. 6, pr.) These two muscles extend laterad and slightly dorsad to their point of attachment to a prong of the tentorium. By their contraction the dorsal wall of the duct is drawn away from the ventral and the salivary secretions are permitted to escape into the mouth.

The circular muscles of the esophagus become greatly enlarged for a short distance in front of the esophageal valve and for some distance back into it (Figs. 14, 15 and 16, sp.) They thus function as a sphincter. The valve is strongly developed, the length of the inflexed portion of the esophagus being about equal to the diameter of the valve. The epithelium and intima of the inflexed portion are unmodified while those of the reflexed portion are much thinner and in longitudinal section appear as two heavy lines with here and there a nucleus in the epithelium (Figs. 14 and 15.) The reflexed portion extends a short distance cephalad to the anterior end of the mid-intestine and so forms a second, a caudally directed, loop. Circular muscles are absent from the caudal portion of the inflexed esophagus and from all of the reflexed portion. Between the inflexed and reflexed portions there is a large blood space, filled with the granular blood plasma and scattered blood corpuscles and traversed by numerous delicate fiber-like outgrowths of the reflexed epithelial cells (Fig. 16, s.) A number of these fibers and anteriorly protruding longitudinal muscles from the mid-intestine, meet the esophagus opposite the anterior end of the sphincter.

The point of union of the fore- and mid- intestine is plainly set off by the striking contrast between the epithelium of the two regions. The thin epithelium, of the reflexed part of the esophagus, gives way to a girdle of large deeply-staining cells, which extend about half the length of the esophageal valve. In longitudinal section from six to twelve large cells are seen to comprise this group on either side (Fig. 15, gl.) The anterior ones are short, polygonal and lie transversely, but farther back they become strongly club-shaped and are directed mesocaudad. The outer ends of the cells are closely appressed while their inner ends are expanded greatly and form a smooth secretory surface. The nuclei are large, with large nucleoli and coarse, deeply-staining chromatin granules, and lie in the expanded inner portion of the cells. These cells are glandular in nature. They stain far more intensely with haematoxylin than any other cells of the alimentary canal. They are granular and finely vacuolate toward their inner margins, where a thin layer of granular substance is to be seen (Fig. 18, p. m.) The inner margin of this granular layer hardens to form a delicate elastic peritrophic membrane which is continually fed back into the mid- and hind-intestine to envelope the food material. This membrane may be seen as a delicate envelope surrounding the excrement as it is thrown off. In some preparations the formation of the peritrophic membrane from the granular secretion can be seen very distinctly with the 1-12 immersion objective.

There are several views as to the origin of the peritrophic membrane in insects. By Pagenstecher ('64), it was thought to be a product of the salivary glands. Frenzel ('85) thought it was a product of the mid-intestinal epithelium. Simpson ('00) in an unpublished paper described it as a product of the mucus cells in Clisiocampa. Schneider ('87) considered it a chitinous prolongation from the esophagus. Van Gehuchten ('90) and Cuenot ('95) claimed that a ring of cells just cephalad of the mid-intestine produces it. In the larva of Psychoda alternata there can be no doubt as to the origin of this membrane. The girdle of cells at the anterior margin of the mid-intestine secretes it.

Behind and laterad to this girdle of cells comes a second girdle of glandular cells. In longitudinal sections seldom more than two cells are to be seen (Figs. 13, 15 and 46, c. gl.) They are very large, among the largest found in the alimentary canal, coarsely vacuolate, and have a straw-yellow color when stained with iron-haematoxylin. The nuclei are large, with rather small nucleoli and fine deeply staining chromatin granules. The cells pour their straw yellow secretion, which has a uniform finely granular consistency, into a pouch which opens widely into the lumen and extends latero-cephalad between the two rings of cells as seen in longitudinal sections. This pouch-like structure is simply a deep invagination on the inner surface of the gland.

Caecae are usually present in the larvae of Diptera, especially in the more specialized forms. They may be long, as in the larvae of the blow-fly (Calliphora), but are more often short and inconspicuous. The number of caecae may be two (Ctenophora), four (Tipula, Simulium, etc.) or many as Miall and Hammond ('00) figure for the larva of the Harlequin fly. Vaney ('02) says that in Anthomyia there are four caecae, in Chironomus many, while in Stratiomyia and Tanypus they may be absent. In Tanypus he finds and figures a group of very large vacuolate cells with ectal diverticula which he claims function as caecae. This group of cells is similarly located, and the cells themselves, except for the ectal diverticula, closely agree with those described above for Psychoda. In Psychoda I am convinced that this group of cells is the rudimentary caecal glands. I find it also present in Pericoma. Caecae are said to be entirely absent in the larvae of Lepidoptera, which in this respect would seem to show a relationship between the Psychodidae and the Lepidoptera. There are not wanting a number of other characters which indicate such an affinity.

Behind the caecal gland comes a group of cells very similar to those which secrete the peritrophic membrane (Figs. 14 and 15). The cells stain quite deeply, are elongate and extend meso-caudad. They have numerous vacuoles which usually contain large spherical concretions (Fig. 19, con.) The nuclei are large with distinct nucleoli and intensely staining chromatin granules. The posterior extent of this group is marked by a few greatly elongated cells which project into the lumen (Fig. 14, ep.) It might be supposed that this group of cells assisted the anterior one in the production of the peritrophic membrane but from repeated examination of my specimens no signs of this have been found.

Caudad of this region comes a long stretch of fairly uniform cells. They are very large and cubical or polygonal (Fig. 2, ep.) The ones in front and behind are cubical, while those in the median region are longer than deep. Scattered among the large cells are to be found small slender ones (Fig. 21, ep.) The cells of this region are stained but slightly with iron-haematoxylin, are finely vacuolate, and possess a narrow but distinct striate border. The nucleus is large and the nucleolus and chromatin are sharply differentiated. These cells are secretory but do not take on the greatly elongated condition found in those farther back during most active discharge of secretion.

These large cells grade off posteriorly into a region of tall slender secretory cells (Fig. 2, ep.), comprising the posterior third of the mid-intestinal epithelium. These slender cells are finely vacuolate and have a very strongly developed striate border (Fig. 24, st. b.) The nuclei are small, usually centrally located, with deeply staining nucleoli and chromatin material. During active secretion, groups of these cells increase greatly in heighth and protrude into the lumen, giving to the inner margin of the epithelium a decidedly uneven surface (Fig. 23, ep.) In this respect, this region stands out in sharp contrast with the anterior region of large cells, where their inner margins form almost a straight line. Here and there among these slender cells as well as the larger anterior ones are to be found huge, coarsely vacuolate cells which protrude into the lumen. These have been described as mucus cells (Fig. 46, m. c.)

The striate border is more or less developed throughout the whole length of the secretory part of the mid-intestine, but its greatest development is to be found in the posterior region during active secretion and just before molting. Some of the earlier workers considered the striate border as a chitinous intima perforated by many fine canals. Later work goes to show, however, that it is simply a ciliate border, consisting of non-vibratile cilia, except perhaps in case of Chironomus larvae (Vignon '99). In Psychoda alternata it grades gradually from the vaculate tips of the cells into a clear homogenous border formed by closely appressed fine cilia. So gradual is the gradation and so intimate is the relation between the cell body and the border that I am inclined to agree with Van Gehuchten ('90) that the cilia are continuations of the cells rather than secretions deposited by them upon their inner margin.

The basement membrane is quite distinct throughout the whole length of the mid-intestine (Figs. 22 and 24, b. m.) In places it is considerably thickened. With perfect fixation the basement membrane remains closely connected with the epithelium. It bears on its outer surface, or more often in slight depressions of it, the numerous strands of circular muscles.

In the region of the esophageal valve, and for a short distance caudad, the circular muscles are weak and the strands far apart (Fig. 20, c. m.) But beginning with the region of very large epithelial cells and extending back along it a short distance the bands of circular muscles become much broader and more regularly placed, with intervening spaces equal to the breadth of the bands. These broad bands give way to narrower and more widely separated ones, which continue back to the region of tall slender epithelial cells. Sections of these strands show their breadth to scarcely exceed the diameter of the nuclei of the underlying epithelial cells. At the point where the large epithelial cells give way to the tall slender ones, the strands of circular muscles are greatly crowded together, having the appearance of a slight sphincter (Fig. 22, c. m.) This crowding of the circular muscles covers but a short area and posteriorly gives way to a greater spacing of them, which extends back to the base of the Malpighian vessels.

The longitudinal muscles are not strongly developed in the mid-intestine. They consist of from ten to twelve narrow, flat strands, which fit closely to the surface of the circular muscles (Fig. 21 and 23, l. m.) Opposite the point, where the circular muscles are crowded together, these longitudinal strands are greatly thickened, almost circular in cross section and stand out from the circular bands more distinctly.

Just at the union of the mid- and hind- intestine are the five Malpighian vessels. In cellular structure they much more closely resemble the epithelium of the mid-intestine than that of the hind-intestine, but their glandular function will account for this, however. From embryological studies it has been shown that these vessels are outgrowths from the hind-intestine. At the point of attachment of these vessels with the alimentary canal they have a short, compact and slightly constricted region (Fig. 26, m. t.) Here the cells are large and alternately from opposite sides extend into the lumen of the vessels giving it a zig-zag course. The nuclei of these cells are oval with small nucleoli and fine chromatin granules. This constricted portion gives way to the much expanded, thin-walled reservoir. The epithelium of this region is very thin, with its inner surface delicately fibrillate and with valve-like projections here and there extending into the lumen (Fig. 27, c.) Beyond the reservoir comes the true glandular portion of the vessel which is much constricted and, in life, is charged with a reddish brown pigment (Fig. 27, a and b). Here the lumen is greatly reduced, being almost closed by the finely granular and vacuolate cells. These cells are very long, as can be seen from longitudinal sections, and as shown by some transverse sections, each cell almost completely girdles the tubule, and forces the lumen toward one side, but more often the lumen is centrally located, the cell completely encircling the tubule. The basement membrane is strongly developed throughout the whole length of the tubule. The chitinous intima is slightly developed in the distal glandular portion, but seems to be absent in the basal portion.

The change from the mid-intestine to the ileum of the hind-intestine is a most striking one. The large secretory cells of the mid-intestine give way to the very small cells of the ileum (Fig. 26 and 28, ep.) These first cells are so very small that with the 1-12 immersion they appear as mere thickenings of the epithelium. The nuclei are very small, deep-staining, and without prominent nucleoli. A distinct, thin chitinous intima is present. This thin epithelium extends caudad to a point slightly before the middle of the ileum, where it develops a distinct fold, which extends into the lumen to form an ileal valve (Fig. 2, 29 and 31, il. v.) From this point to the union of ileum and colon, the epithelial cells are much larger, with enormous nuclei, in which the small nucleoli and coarse chromatin granules stain deeply. The ileum is well supplied with muscles. The delicate circular muscles of the mid-intestine are replaced in the ileum by very strong bands which completely clothe it. For a short distance, immediately behind the Malpighian vessels, the circular muscles are absent (Figs. 28-29.) From the point where the circular muscles begin, back to the ileal valve, there are two layers of them. The inner layer of delicate bands serves as a sphincter for the ileal valve, while the outer layer is continuous throughout the hind-intestine (Figs. 29 and 30). From the ileal valve back to the colon the individual bands of the circular muscles are much stronger and more oval than those of the anterior part of the ileum. The longitudinal muscles are only slightly developed in the hind-intestine. From longitudinal sections it would appear that, at the point where the first circular muscles appear, the longitudinal muscles divide to form an inner and an outer layer, but from cross sections only outer longitudinal muscles appear in front of the ileal valve. Three strong, and two or three smaller strands appear clustered together along either side of the canal. From the ileal valve to the colon these same lateral clusters of outer longitudinal muscles appear as well as scattered inner strands between the circular muscles and epithelium (Fig. 32, l. m.)

Posteriorly the constricted ileum projects into the expanded colon so as to form a slight valve (Figs. 2 and 33, v.) Just in front of this valve is a strong sphincter composed of five or six strong strands of circular muscles. The colon is slightly shorter than the ileum but its diameter is twice as great. Its epithelium is very thick, consisting of large cubical cells, of uniform finely granular nature, with distinctly striate inner curving margins which project into the lumen (Figs. 35 and 36, ep.) The cell walls are seldom distinct to the base. The nuclei are very large, and oval, with large nucleoli and fine chromatin granules. The basement membrane is very delicate and difficult of detection in most preparations. The circular muscles are strongly developed and are so fitted into pockets in the epithelium that their outer surface is just even with that of the epithelium (Fig. 36, c. m.) Longitudinal muscles have not been observed either in longitudinal or cross sections of the colon as well as the rectum. Sections of close-fitting nerve fibers were at first mistaken for longitudinal muscles. The chitinous intima is but slightly developed and closely adheres to the epithelium. Along the surface of the intima and especually down in the grooves between the cells is a layer of a finely granular deposit which stains blue with haematoxylin. This deposit is present in all of my preparations, which together with the enormous development of the epithelium, would suggest some association with absorption and I am of the opinion that in this larva much of the absorption of digested food takes place here.

The circular muscles of the anterior end of the rectum are much more strongly developed than are those of the colon (Fig. 37, c. m.) They lie on the surface of the epithelium and form a continuous layer. Farther caudad the individual bands decrease in strength rapidly. These circular muscles form a sort of sphincter about the rectum. The nuclei of the circular muscles are very large and are surrounded by undifferentiated protoplasm. The basement membrane is more strongly developed than in the colon. The epithelium is greatly reduced especially in the caudal portion where the cells are long and thin except opposite the nuclei, where they are thickened so as to protrude slightly into the narrow lumen. In the anterior region of the rectum the epithelium is thrown into six longitudinal folds (Fig. 37, ep.) The epithelium of the rectum is continuous with that of the four slightly eversible anal papillae, where it becomes much thicker and the cells more vacuolate. The chitinous intima of the rectum is much heavier than that of the colon and its thickness increases toward the anus where it is continuous with the chitin of the anal papillae (Fig. 2, a. p.)

MORPHOLOGICAL CHANGES IN THE EPITHELIUM OF THE MID-INTESTINE.

In insects the changes, which the epithelium of the mid-intestine undergoes, are associated either with the pouring out of digestive secretions at the time of feeding or with the larval molting periods. These changes are marked by total or partial epithelial degeneration and regeneration. In the present work, special efforts have been made to get as complete series of larvae as possible in order to show the changes accompanying feeding and molting. By means of carefully timed starvation and feeding experiments, all desired stages associated with the feeding period were easily obtained. But it was much more difficult to get all the stages at the molting period, since the morphological changes in the mid-intestine are largely completed before the skin is cast and there is practically no forewarning as to just when the transformation begins. Only by means of a large series of specimens taken during the inactive period preceding and following the casting of the skin was it possible to get all the desired stages of transformation.

Changes Accompanying Feeding.

The extent of degeneration and regeneration of the epithelium of the mid-intestine, at the time of feeding depends upon the type of secretion found in the epithelial cells. Where the holocrine type of secretion prevails, partial or even total degeneration and renewal of the epithelium will follow each full feeding, while with the merocrine type only slight or no renewal will be found since the epithelial cells are not destroyed by the discharge of secretions.

The nymphs of dragonflies and adult water beetles, in which may be found the holocrine type of secretion, are excellent examples for the study of epithelial regeneration following feeding. Needham ('97) found that, in case of dragonfly nymphs, after prolonged fasts of two months, the cells became so gorged with digestive secretions that the epithelium became twice the height of the normal and when food was taken in practically all of the cells were destroyed by the process of excretion and a complete new epithelium formed from scattered nidi or regenerating centers. Frenzel ('85), Vangel ('86), Bizzozzero ('93) and Rengel ('97) described even more striking cases of epithelial degeneration and regeneration in adult water beetles of the genera Hydrophilus, Hydrobius, Hydrous and Cybister. These beetles like the nymphs of dragonflies, feed intermittently, being able to fast for periods when food is not at hand and then when food is abundant, devouring great quantities of it. In these bettles the entire epithelium with its basal chitinous membrane is described as being cast off after each full feeding. The new epithelium is quickly developed from highly specialized regenerating centers or nidi, which protrude through the muscular coat of the canal, to form distinct diverticula.

The merocrine type of secretion is found in the mid-intestinal epithelium of those insects which feed continuously and which require a continuous supply of digestive fluids. In these forms the cells are always active, the extent of the secreting activity depending upon the extent of feeding. But since the cells are not destroyed by secretion and excretion there is no occasion for any regeneration in connection with the intake of food and digestion. This type of epithelial secretion was described by Van Gehuchten ('90 and '93) for Ptychoptera contaminata, there being no epithelial regeneration associated with digestion. Folsom and Wells ('06) describe this as the prevailing type of secretion in the mid-intestine of Collembola, there being no regeneration at the time of feeding.

Psychoda alternata in its larval state is not an intermittent feeder but is most at home at the mouth of open sewers, in cultures of decaying horse manure or other vegetable ferments, where it finds abundance of food always present. An occasional plankton form may be found mingled with the food but the bulk of the intestinal contents consists of bits of decayed vegetation. The larva is a voracious feeder and extremely active, scarcely refraining from feeding long enough to molt. The canal always has a great quantity of food material in it, even at the molting periods. From careful study of the epithelium of the mid-intestine of this form, I find the merocrine type of secretion prevailing and an absence of epithelial regeneration associated with feeding.

In hopes of being able to study to better advantage the type of secretion and of better understanding the relation of its discharge to the intake of food, I undertook a series of feeding experiments. Larvae were placed in small glass vessels with clean tap-water and kept there without food for periods varying from one to twelve days. The larger larvae invariably pupated before the experiments could be completed, so it was necessary to use larvae which were less than half grown. Larvae that had fasted for varying periods up to twelve days were killed and sectioned for determining what changes, if any, the mid-intestinal epithelium underwent during the fasts. Likewise larvae starved for two, three, four, seven and twelve days were removed to vessels containing abundance of food, and then after feeding for periods varying from half an hour up to seven hours, they were killed and sectioned for studying the epithelial changes accompanying feeding.

From a study of the preparations made from these larvae it was found that where the fast was prolonged more than four days, the mid-intestinal epithelium became so reduced and weakened that it failed to recover even though the larva survived the fast and fed freely for a time (Fig. 40). Simpson ('01, in an unpublished paper) found a similar degeneration of the epithelial cells of the mid-intestine of Clisiocampa larvae that had fasted for five days. When the fast is prolonged four days the cells take on a distinct vacuolate appearance associated with a heavy discharge of secretion (Fig. 39). After six or seven days this vacuolate condition has disappeared and the cells become greatly reduced in height. They almost cease to excrete digestive fluids and the striate border is then more conspicuous. Aside from a continued reduction in the height of the epithelium, and a greater shriveling of the cells, no further marked changes are brought about, the cells finally dying. At no time, even after a twelve day fast, is the mid-intestine completely free from food material. As a consequence there is a constant stimulus to the excretion of the digestive secretion and as the fast is prolonged the finely granular secretion is poured out and soon comes to fill most of the space between the reduced epithelium and the food content of the canal (Fig. 39, d. sec.) In place of the secretion being stored up in the cells as in the nymphs of dragonflies, it is continually poured into the lumen. This process soon drains the cells of their vitality, since but little real nourishment can be absorbed from the already thoroughly digested content of the canal.

With larvae that had fasted less than four days no marked changes were found in the mid-intestinal epithelium. The food content of the canal is sufficient, apparently, to sustain the larva and to stimulate the cells of the epithelium to normal activities for this period so that when a fresh supply of food is taken in normal digestion is continued (Fig. 41). From the results of these expreiments, which comprised upwards of fifty separate lots of larvae, it was found necessary to turn to the preparations of the normal feeding larvae, for the determination of the type of secretion and the relation of its discharge to the intake of food.

For some time, the changes in the mid-intestinal epithelium just preceding the casting of the larval skin were mistaken for signs of an excessive production and storing of secretions, but when series of larvae preparing to molt were studied the mistake was detected. In this larva there are four sources from which the digestive secretions of the mid-intestine are derived.

As previously noted, the gastric caecae, usually present in the higher Diptera, are replaced in Psychoda alternata by a greatly reduced caecal gland which girdles the mid-intestine in the region of the esophageal valve. The large cells of this gland produce a yellowish digestive secretion similar to that of the gastric caecae of other insects. During most active secretion of these caecal glands, the cells become swollen and finely vacuolate (Figs. 18 and 47, c. gl.) The pouch, into which the secretion is poured, becomes so completely filled that its neck appears to flare, leaving a wide exit of the secretion into the lumen. During less active secretion and excretion the cells become somewhat reduced, the vacuolation less distinct and the pouch less distended with secretion or even almost empty. This is one source of digestive secretion.

A second source is the long stretch of very large cells caudad of the esophageal valve (Fig. 2, ep.) These cells during active secretion and excretion give off a finely granular secretion. This secretion is not given off as globules or droplets but simply oozes through the thin striate border of the large finely vacuolate cells and comes to fill all the space between the epithelium and the peritrophic membrane (Fig. 42). This is perhaps the most abundant supply of digestive secretion found in the mid-intestine of this form.

Just caudad of the point where the region of large cells gives way to that of the tall slender ones, comes a group of cells which during active secretion becomes greatly elongate and protrude into the lumen. These cells are active in throwing off small spherical bodies of their protoplasm by the pinching off of their tips, which float out into the lumen to dissolve and form a third supply of digestive secretion (Figs. 43 and 44, sec. p.)

The fourth source of digestive secretion is the less elongate epithelial cells farther caudad. These cells are more granular and vacuolate next to the striate border and throw off distinct globules which collect along the margin of the striate border (Fig. 45, sec. g.) These globules seem to burst and give out a secretion similar to the finely granular material of the anterior part of the mid-intestine. The striate border becomes less distinct where the cells are actively secreting and excreting but is never completely obliterated.

The mucous cells of Leidig ('57), Frenzel ('82 and '85), Korotneff ('85), Beauregard ('86), Fausseck ('87), Mingazzini ('89), Balbiani ('90), and Simpson ('00 in unpublished paper) are present in this larva. They are scattered among the large secretory cells of the anterior region as well as among the tall slender cells of the posterior region. As compared with the surrounding cells they are truly monsters (Fig. 46, m. c.) They are connected with the basement membrane by a constricted pedicle while the distal end is enormously expanded and protrudes into the lumen. They are coarsely vacuolate throughout but especially so toward the inner end. The nucleus is scarcely larger than those of adjoining cells, and does not differ from them in the arrangement of nucleolus and chromatin material. Some writers have attributed to these cells the function of secreting the peritrophic membrane, others claim that their secretion serves as a lubricant. In the larva of Psychoda alternata these cells certainly have nothing to do with the secretion of the peritrophic membrane. The fact that the secretion of these cells resembles that from surrounding cells microscopically, that their greatest activity corresponds with that of the surrounding cells and the fact that the food, enveloped in the peritrophic membrane, is continually floated, so to speak, in digestive fluids, cause me to hesitate to accept the view that the secretion of these cells is merely a lubricant. I am inclined to believe that here we have simply specialized digestive cells.

The slender cells, of the region immediately caudad of the caecal glands, have a coarse granular and finely vacuolate structure. In some preparations a slight discharge of granular secretions is to be seen although this is more frequently absent. The striate border is only slightly developed. Between the middle and distal margin of these cells are to be found vacuoles of various sizes which inclose dark brown concretions (Figs. 19 and 47, con.) These concretions are spherical, almost completely filling the vacuoles and very dense. I have not found them in any of the other epithelial cells of the mid-intestine of this larva. They closely resemble those found by Folsom and Wells in the mid-intestinal epithelium of Collembola, and are probably waste products which are secreted and held by these cells until the molting period when they are discharged along with the cells. If my interpretation of these concretions is correct these cells have a definite excretory function.

Passing forward to the anterior region of the mid-intestine we find the cells which produce the peritrophic membrane. These cells are especially active during feeding. They appear long, club-shaped and become finely vacuolate on their inner margin. From them is discharged a finely granular secretion, which forms a narrow inner border to the cells (Figs. 18 and 47, p. m.) It is difficult to tell just where the cell-body ends and the layer of secretion begins. On the inner surface of this border a portion of it hardens to form the thin uniform peritrophic membrane which closely resembles the chitinous intima of the esophagus. From the reaction of these cells to stain it is evident that they are secreting continuously; but the underlying border of secretion is especially prominent at certain times. The course of most active secretion seems to pass along the canal like a wave, following the entrance of a new supply of food somewhat as found in dragonfly nymphs. By the time the discharge of secretions in the posterior part of the mid-intestine has reached a maximum it has begun to decrease in the anterior portion. This is the case with the cells producing the peritrophic membrane as well as those of the caecal glands.

Changes at the Molting Periods.

It is well known that, with each larval molt, the entire outer cuticula, as well as the intima of the fore- and hind-intestine and the tracheal system, are cast. Sharp ('95) maintains that the facilitation of growth by the casting of the chitinous coat is only of secondary importance. The discharge of the chitinous coat is merely an outward sign that internal changes have been going on. Eisig ('87) suggests that since chitin is a nitrogenous substance, perhaps the casting of the chitinous coat is a means of disposing of nitrogenous wastes, to which Sharp adds that perhaps the same is true of carbonaceous wastes. If the casting of the exuviae has an excretory function associated with it and if the epithelium of the mid-intestine has an ectodermal origin, as believed by some writers, then it will be easier to explain certain morphological changes which occur in the mid-intestinal epithelium at the time of molting. The striking morphological changes undergone by insects at the time of pupation and emerging of the adult, are well known and have been given much attention by workers, but there are similar although perhaps less intensive changes at each larval molt, which have been almost entirely overlooked. We shall now consider the changes in the mid-intestinal epithelium at the time of molting.

Folsom and Wells' ('06) work on epithelial degeneration, regeneration and secretion in the mid-intestine of Collembola deals primarily with the changes in the digestive epithelium at the molting periods. The Collembola are among our most primitive forms of insects, lacking Malpighian vessels and developing without obvious metamorphosis. With this type of development we should expect to find equivalent morphological changes at the different molting periods. Conditions found in the study of a form of this generalized type will not necessarily be like those in higher forms but are suggestive for one making a study of any more specialized form.

The normal epithelium of the mid-intestine of Collembola was found to be composed of very large granular and finely vacuolate cells. At the approach of an ecdysis the cells begin elongating and the inner half becomes more vacuolate. As this vacuolation continues, any concretions and gregarine parasites present in the cells and about half of the nuclei migrate from the more dense portions of the cells into the inner, more vacuolate region. Then comes a cutting off of the inner half of the epithelium. During these changes cell walls are obliterated. A new striate border forms along the line of constriction and the inner portion of the epithelium is cast into the lumen where it is digested. To replace the nuclei lost by the sloughing off, those remaining undergo mitotic division, cell boundaries reappear and the normal epithelium is again restored. Since the forms studied lacked Malpighian vessels, Folsom & Wells concluded that this periodical discharge of half of the epithelium with concretions, inclusions and parasites had an excretory function similar to that of the Malpighian vessels in other insects. The short inactive period preceding each molt made it possible to get any desired stage of transformation. Here we find only partial epithelial regeneration at each molting period.

We shall now consider a more specialized type of insect, one with complete metamorphosis, and see how the changes in the mid-intestinal epithelium at the time of the larval molts compare with those in Collembola at the molting periods. Mobüsz ('97) studied the changes in the mid-intestinal epithelium of Anthrenus during the larval molts and found that the same changes appeared then as at pupation, only less intensive. In the study of his preparations, which included larvae in various stages of transformation, he found a large mass of material in the lumen of the mid-intesine which he first mistook for parasites. Further studies revealed to him that this inclusion was simply the remains of the sloughed off epithelium. He was able to find various stages in the throwing off of the old cells from that in which, by muscular contraction and development of the new epithelium, the old with its basement membrane was separated from the muscular coat, to that in which it was cast into the lumen and digested leaving its residue enveloped in the resistant basement membrane. Mobüsz takes exception to Rengel's work on Tenebrio molitor ('96) where he describes the nidi as being cast off with the old epithelium and basement membrane and later making their way through the basement membrane and regaining an attachment to the muscular coat. Rengel must certainly have had faulty preparations. Mobüsz found the nidi retaining their attachment with the muscular coat and concluded that either, the cells of the nidi being embryological, no basement membrane was produced beneath them, or if produced it was dissolved so that it would slip off over them when it was cast off with the old epithelium. By multiplication the cells of the nidi quickly produce the layer of new epithelium. In fact these first changes are produced with such rapidity that Mobüsz failed to catch them in any of his specimens. The new epithelium soon developes its basement membrane and striate border and in time the nidi take on their normal condition and the new epithelium is mature. Here we find the epithelium cast off bodily and not merely in part. In conclusion Mobusz maintains that:

(1) At each larval molt there is a total regeneration of the epithelium of the mid-intestine.

(2) The transformation of the mature larva to the pupa, in the holometabola, is simply an intensified larval molt and we may expect the same morphological changes, although to varying degrees, perhaps, at these periods.

(3) He believes that there is not only total regeneration of the mid-intestinal epithelium but also that there are greater or less changes in the epithelium of the fore- and hind-intestine and in the muscular and adipose tissues of the larva.

The larva of Psychoda alternata on preparing to molt, ceases feeding for a short time and to a marked degree discharges the food content from the alimentary canal. Then comes a short period of inactivity followed by pronounced peristalic contractions. In the thoracic region a strong ventral flexure occurs and then peristaltic waves of contraction pass forward from the posterior end of the body. This may be repeated a number of times before the chitin bursts on the dorsum of the first two thoracic segments and the larva crawls out. As soon as the larva is free it becomes quite active and begins to feed. These outward signs of transformation are simply the culmination of the metamorphosis. The internal changes are practically completed before the larval skin is cast.

Shortly before the time of molting the mid-intestinal epithelium begins to undergo striking changes. The cells begin to elongate and protrude into the lumen. Their distal halves become distinctly vacuolate (Fig. 48). There is to be noted in the nuclei themselves some change. The chromatin usually disappears or comes to closely envelope the nucleolus. At this stage the cytoplasm and enclosed secretions of the cells stain intensely with iron haematoxylin which can be removed only by prolonged differentiation.

This stage in the metamorphosis was first observed in a larva that had fasted for three days and was thought to be due to the storing up of digestive secretions, but when other specimens from the same lot were examined and no signs of such development found and when larvae, that were known to be ready to molt, were examined and the same identical conditions found, the theory of stored up secretions was discarded. This condition of degeneration of the mid-intestinal epithelium has also been found in some specimens collected at random for general structural work, they having been caught in the act of transformation.

A later stage shows these epithelial cells becoming more broken up by large vacuoles. The entire distal portion of the cells becomes vacuolate with strands of cytoplasm surrounding the vacuoles (Fig. 49). The vacuoles at first circular in section become irregular in shape as their size increases, while the nuclei are found moving out into the distal more vacuolate portion of the epithelium. All signs of cell boundaries are lost and the epithelium resembles a mass of ragged cytoplasm with nuclei scattered about through it. In the cytoplasm small round concretions are usually present in great abundance, especially in the more vacuolate portion (Figs. 48 and 49, con.) Gregarine parasites are seldom found within the epithelium. The nuclei degenerate unevenly. Some near the basement membrane may retain a more healthy appearance with chromatine granules and large nucleolus, while those beginning to migrate lose their chromatin. At this stage of degeneration, there appears in the lumen of the mid-intestine, surrounding the peritrophic membrane and enveloped food contents, a great mass of finely granular and deeply staining secretion which is evidently the product of the degenerating cells of the epithelium. This deposit seems to be confined largely to the posterior half of the mid-intestine where the epithelium consists of the tall slender cells. In this bluish-staining deposit are to be seen scattered remains of degenerating nuclei, especially nucleoli, which seem to be especially resistant. Scattered through this deposit are also to be found deeply staining bodies, probably concretions, and a quantity of uniform yellowish secretions, evidently a product of the degenerating cells.

This degeneration of the mid-intestinal epithelium begins in the posterior portion where the cells are long and slender and as metamorphosis advances, the process of degeneration may be traced forward to the esophageal valve (Figs. 50 and 51). When the large cells of the anterior half of the mid-intestine have become strongly vacuolate, those of the posterior part have almost completely broken down and their contents cast into the lumen. The method, by which the midintestinal epithelium, in this form, is cast off, in no wise resembles that described for Hydrophilus, after feeding, where the epithelium with its basal chitinous layer is cast off bodily; nor is it so complete and regular as that described by Mobüsz for Anthrenus. It more nearly resembles the degeneration of the mid-intestinal epithelium of dragonfly nymphs after feeding. The individual cells themselves break down and are sloughed off rather than the epithelium in mass being cast into the lumen.

The extent to which this degeneration takes place is not always easy to determine. It can be followed to where practically all of the old nuclei have migrated out into the lumen and degenerated (Fig. 51). And where practically all of the cell content is dissolved, although for a time, at least, a quantity of the cytoplasm remains in contact with the basement membrane, which is not cast off. I am inclined to believe that this is as far as the degeneration of the mid-intestinal epithelium proceeds in this form. The old adhering cytoplasm is apparently absorbed by the newly developing epithelium.

Between the epithelium of the mid-intestine and its underlying basement membrane are to be found numerous very small regenerating cells from which the new epithelium is developed (Figs. 48, 49, 50, 51, r. c.) These small cells are extremely difficult of detection except at the time of transformation. Cell division takes place in these embryonic cells while their diameter is yet scarcely one-fifth that of the nucleus of mature epithelial cells, so that it is extermely difficult to make out the type of division, but from a study of my preparations it would seem that here we have direct cell division (Fig. 54). They may be collected in small groups or in pairs or scattered singly along the basement membrane. The first structure that can be defilitely made out is the deeply staining nucleus, but as the degenration of the old epithelium advances, a definite cell form can be distinguished. The cytoplasm at the beginning is a mere border about the nucleus, but as development advances it rapidly increases in bulk and comes to form a distinct cell body about the nucleus. By the time the old epithelium is nearly all sloughed off these new cells have come to protrude up into the adhering cytoplasm of the old cells, which they seem to absorb in part (Fig. 51, r. c.)

These conditions of degeneration and regeneration of the mid-intestinal epithelium are found in larvae previous to the casting of the larval skin. Changes at this point take place with very great rapidity so that it is easy to see how former workers came to overlook, almost completely, this degeneration and regeneration of the mid-intestinal epithelium at the larval molting periods.

In larvae, taken immediately after the casting of the skin, the new epithelium of the mid-intestine is already developed. At first the cells are low and stain deeply with iron haematoxylin (Fig. 52, ep.). The nucleoli are large and stain deeply, while the chromatin material is not distinctly made out. The cytoplasm is coarsely granular and has the appearance of being striated next to the lumen. The striate border is developed early and appears even more distinct than in later stages when the cells have begun to secrete (Figs. 52 and 53, st. b.)

The contents of the mid-intestine, not cast off before metamorphosis began, is still found to be enclosed in the resistant peritrophic membrane and occupies the central portion of the lumen. Between this central mass and the new epithelium, there is still to be found a great quantity of the finely granular yellowish product from the degenerate epithelium. Occasionally the sloughed off intima of the esophagus is found coiled about in the mid-intestine, but the degenerate epithelium of the mid-intestine is so completely dissolved that only the slightest traces of it are to be found after the skin has been cast.

In this way the epithelium of the entire mid-intestine, including the caecal glands and the group of cells which produce the peritrophic membrane, is renovated at each larval molt. As soon as the metamorphosis is completed and the skin cast off the larva resumes activity and begins to feed again. The new cells of the mid-intestinal epithelium at once respond to the demand made upon them for secretions and the larva enters upon the next stage of its development.

CONCLUSIONS.

The alimentary canal of the larva of Psychoda alternata is a generalized one in conformity with the habits of the larva. Both the fore- and hind-intestine are relatively short while the mid-intestine makes up at least two-thirds of the entire length of the canal.

Longitudinal muscles are absent in the fore-intestine and in the colon and rectum.

Gastric caecae are replaced by a caecal gland, which girdles the median portion of the esophageal valve.

There are five Malpighian vessels of similar form and structure, two extending cephalad and three caudad.

The rectum is prolonged into four slightly eversible papillae, which are homologous with the anal tracheal gills of Culex and related forms.

The epithelium of the mid-intestine is divided into five distinct regions; an anterior one giving rise to the peritrophic membrane, a caecal gland, a small area of long glandular cells, a long stretch of large polygonal cells, and the posterior region of tall slender cells. The so-called mucus cells are abundant. There is no regeneration of the epithelium of the mid-intestine at the time of feeding. During a fast, secretions are not stored up in the epithelial cells but are continually poured out and if the fast be prolonged the cells may completely break down. The peritrophic membrane is secreted by a definite group of cells at the anterior end of the mid-intestine.

At each larval molt the epithelium of the mid-intestine is completely renewed. The old cells are not cast off as a whole, but the degeneration begins next to the lumen and continues until the whole cell is broken down. This degeneration begins in the posterior region of the mid-intestine and proceeds forward.

Regeneration is from scattered embryonic cells which lie in the angles at the base of the epithelial cells. The regenerated epithelium of the mid-intestine is mature by the time the larval skin is cast off.

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LIST OF ABREVIATIONS.

a. p., anal papillae.
b. c., blood corpuscles.
b. m., basement membrane.
br., brain.
c., concretion bearing cells.
c. gl., caecal gland.
c. m., circular muscles.
col., colon.
com., commissure.
con., concretion.
d., salivary duct.
d. c., degenerating cells.
d. sec., digestive secretion.
ep., epithelium.
eph., epipharynx.
es., esophagus.
es. v., esophageal valve.
f., food.
gl., gland which secretes the peritrophic membrane.
hy., hypopharynx.
il., ileum.
il. v., ileal valve.
in., intima.
l., lumen.
la., labium.
l. m., longitudinal muscles.
lr., labrum.
m., mouth.
m. c., mucus cell.
md., mandible.
m. int., mid-intestine.
m. t., Malpighian tubule.
mx., maxilla.
mx. p., maxillary palpus.
n., nucleus.
nl., nucleolus.
n. m., nuclear membrane.
p., caecal gland pouch.
ph., pharynx.
ph. b., pharyngeal bars.
ph. m., pharyngeal muscles.
pr., press of salivary duct.
r. c., regenerating cells.
rec., rectum.
s., blood space.
sec. c., secretory cells.
sec. p., secretory proliferations.
s. g., salivary gland.
sp., sphincter.
st. b., striate border.
vac., vacuole.
v., valve between ileum and colon.

EXPLANATION OF PLATES.

PLATE XLIV.

1. Alimentary canal in surface view.

2. Longitudinal section of alimentary canal.

3. Mouth parts.

4. Anterior end of larva with alimentary canal and nervous system in situ.

5. Longitudinal section through the anterior portion of the head.

6. Transverse section through the anterior end of the pharynx. Plane of section sloping slightly dorso-caudad.

7. Transverse section through the median portion of the pharynx. Plane of section sloping slightly dorso-caudad.

8. Portion of the transverse section through the pharynx in the region of the large lateral pharyngeal muscles.

9. Transverse section through the caudal region of the pharynx.

10. Transverse section through the anterior region of the esophagus.

11. Transverse section through the anterior end of the esophageal valve. Plane of section sloping slightly dorso-caudad.

PLATE XLV.

12. Longitudinal section of salivary gland.

13. Transverse section through the middle of the esophageal valve. Plane of section sloping slightly cephalad to the right.

14. Longitudinal section of esophageal valve.

15. A portion of longitudinal section of esophageal valve.

16. Longitudinal section of cephalic end of esophageal valve showing a portion of the blood space.

17. Longitudinal section through the tip of the infolded portion of the esophagus, showing chitinous spines.

18. A portion of a longitudinal section through the region of the caecal gland.

19. Cells with enclosed concretions, from the region immediately caudad of the caecal gland.

20. Longitudinal section through the region at which the concretion-bearing cells give way to the large polygonal digestive cells.

PLATE XLVI.

21. Transverse section of mid-intestine through the region of large polygonal digestive cells.

22. Longitudinal section through the region at which the polygonal cells give way to the tall slender ones.

23. Transverse section of mid-intestine through the region of tall slender cells.

24. Longitudinal section through the region of tall cells.

25. Transverse section through the region at which the Malpighian vessels join the alimentary canal.

26. Longitudinal section through the same region.

27. Transverse sections of Malpighian vessels. (a and b) Through the pigmented secretory portions, (c) through the basal reservoir.

28. Transverse section of the ileum immediately caudad of the Malpighian vessels, showing absence of circular and longitudinal muscles.

29. Longitudinal section of the anterior portion of the ileum.

Plate XLVII.

30. Transverse section through the ileum just cephalad of the ileal valve.
31. Longitudinal section through the ileal valve.
32. Transverse section through ileum, caudad of the ileal valve.
33. Longitudinal section through the valve between the ileum and colon.
34. Transverse section through the valve between the ileum and colon.
35. Transverse section through the colon.
36. Portion of longitudinal section through the colon.
37. Transverse section through the rectum.
38. Longitudinal section through the rectum and anal papillae.

XLVIII.

Epithelial secretion and regeneration (with 1-12 immersion.)

39. Epithelial cells of the mid-intestine of a larva after a four days' fast.

40. (a) Epithelial cells of the mid-intestine of a larva after a seven days' fast. (b) Same after feeding half an hour.

41. Epithelial cells of mid-intestine of a larva that had fasted two days then fed for half an hour.

42. A single large polygonal digestive cell from the anterior portion of the mid-intestine.

43. Tall slender epithelial cells discharging digestive proliferations.

44. Same, from region slightly cephalad of (43).

45. Epithelial cells from the posterior region of the mid-intestine discharging globules of digestive secretion.

46. Mucus cells from posterior region of mid-intestines.

47. Longitudinal section through the caecal gland.

48. Epithelial cells from the anterior portion of the mid-intestine shortly before molting, showing the first stage of epithelial degeneration.

49. Epithelial cells showing a later stage of degeneration.

50. Epithelial cells from anterior portion of mid-intestine showing the process of degeneration well under way.

51. Epithelial cells from the same larva, but from the region of tall slender cells with degeneration almost complete.

52. Newly regenerated epithelium of the mid-intestine of a larva that had just emerged from the larval skin.

53. Epithelium of the mid-intestine of a larva that had molted less than a day previous to killing.

54. Embryonic cells in various stages of development.